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The Migratory Whale Herd Concept: A Novel Unit to Conserve under the Ecological Paradigm

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ABSTRACT

Photographic and genetic studies have revealed the complex behavior of migratory large whales. Most research and management is geographically based, focusing on either wintering or summering areas, which in most cases fails to capture this complexity. We use examples from humpback whales (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*) to illustrate the concept of migratory herds, which we define as conspecific whales that migrate between the same wintering and feeding ground. In cases where individuals show strong fidelity to both feeding and wintering grounds, and therefore to a herd, dispersal between herds can be low enough to render them as demographically independent populations, where population dynamics are determined more by net internal recruitment (births minus deaths) than by immigration from outside sources. In these cases, the migratory whale herd is the appropriate unit to conserve under the ecological paradigm that focuses on groups united by demographic forces. We suggest that when addressing questions focused on ecological timescales for whale species with maternally-learned migratory routes and strong fidelity to migratory destinations, the migratory whale herd is a better initial working hypothesis than one based on geographically defined strata.

KEYWORDS

Management unit, demographic independence, cetacean, migration, population structure, humpback whale, gray whale

1 | INTRODUCTION

The term 'population' has no single definition, yet populations are fundamental to most studies in ecology, demography, and evolution, and are the foundation of conservation management. In recent decades there has been a growing recognition that the definition of a population should depend on the type of question being asked (Palsbøll et al. 2007, Taylor & Dizon 1999, Waples & Gaggiotti 2006). For example, the population that is relevant to a study of dietary patterns of California sea lions (DeLong et al. 1991) is very different from the population that is relevant to understanding the evolutionary history of that species (Schramm et al. 2009). Waples and Gaggiotti (2006) review different population concepts and classify them into two broad categories, the 'Ecological Paradigm' and the 'Evolutionary Paradigm'. Those that focus on groups that are united by demographic forces (e.g., dispersal of animals between groups, birth and death rates within groups, and other forces that operate on an annual timescale) fall under the Ecological Paradigm; those that focus on groups united by evolutionary forces (e.g., gene flow, selective pressure, and other forces that operate on the timescale of generations or longer) fall under the Evolutionary Paradigm.

The laws and frameworks that guide conservation and management can also be classified as falling under the Ecological or Evolutionary Paradigms, depending on their management objectives (Martien et al. 2013, Palsbøll et al. 2007, Taylor et al. 2010). The two primary laws governing the conservation and management of marine mammals in the United States are the Endangered Species Act (ESA) and the Marine Mammal Protection Act (MMPA). Law that focus on preventing extinction, like the ESA, clearly fall under the Evolutionary Paradigm. The MMPA, in contrast, has as its stated objectives maintaining populations as

‘functioning elements of the ecosystems of which they are a part’ and preventing their abundance from falling below ‘optimal sustainable population levels.’ This focus of the law on ecological and demographic features of populations places it firmly under the Ecological Paradigm.

The MMPA requires that all marine mammals in U.S. waters be divided into ‘population stocks’ (henceforth, ‘stock’) for management purposes. Specifically, the Guidelines for Assessing Marine Mammals under the MMPA say that:

...stocks should ideally be comprised of a single Demographically Independent Population (DIP), where demographic independence means that the population dynamics of the affected group is more a consequence of births and deaths within the group (internal dynamics) rather than immigration or emigration (external dynamics) (Moore & Merrick 2011).

A DIP is the population concept relevant to research questions focused at ecological scales, such as estimating vital rates, trends in abundance, and metrics of population health. As such, the concept of DIPs has subsequently been recognized for conservation and management efforts on ecological timescales (Martien et al. 2012, Palsbøll et al. 2007).

Evaluating whether groups constitute DIPs requires determining whether the rate of dispersal between them is low enough to render them demographically independent (Hastings 1993, Palsbøll et al. 2007, Taylor 1997, Taylor & Dizon 1999, Waples & Gaggiotti 2006). The DIP Delineation Handbook (Martien et al. 2019) provides an extensive review of the various methods and data types that can inform such a determination once putative DIPs have been identified. However, in some cases, deciding how to stratify individuals into putative DIPs can

be challenging. This is particularly true for whale species that undertake annual migrations between high-latitude feeding grounds, where they spend the majority of the year, and low-latitude wintering grounds, where most breeding has been assumed to occur. The complicated annual movement patterns exhibited by these species can result in wintering grounds that are comprised of individuals from multiple feeding grounds, and feeding grounds that are shared by individuals from different wintering grounds (e.g., Calambokidis et al. 2000, Calambokidis et al. 2001, Clapham et al. 1993b, Urbán 2019).

Most migratory whale research has focused on either wintering grounds (e.g., Carroll et al. 2012, Carroll et al. 2016, Carroll et al. 2011, Darling et al. 2019, Kershaw et al. 2017) or feeding grounds (e.g., Clapham et al. 2008, Frasier et al. 2011, Lang et al. 2014, LeDuc et al. 2007). While these are valid stratifications that are relevant to many questions, in many cases neither feeding nor wintering grounds represent demographically cohesive or independent units. This is particularly true in species where calves learn their migratory routes from their mothers and exhibit strong fidelity to both feeding and wintering grounds throughout their lives, and where such grounds are used by animals from multiple geographic regions at the other end of the migration.

Here we present a new concept called the ‘migratory whale herd,’ which we define as, “conspecific whales that migrate between the same wintering and feeding grounds”. Migratory whale herds do not move together as a single cohesive group, as is seen in some ungulates, but simply utilize the same migratory destinations. Because recruitment into migratory whale herds is based on maternally directed learning of the migratory route, and all members of the group are exposed to the same environmental conditions and threats throughout the year, they

represent the natural demographic unit for migratory whales and are therefore a special case of a DIP. We recommend that research and management that falls under the Ecological Paradigm (Waples & Gaggiotti 2006) should be focused on migratory herds for at least some species of large whales.

We illustrate the migratory whale herd concept by focusing on the humpback whale (*Megaptera novaeangliae*), data for which suggested this new way of thinking about DIPs for migratory animals. We then discuss gray whales (*Eschrichtius robustus*), which also exhibit migratory patterns consistent with the migratory whale herd concept. Drawing upon life history and behavioral traits of these two species, we conclude that the 'herd' concept might prove to be a better initial working hypothesis for some migratory baleen whales than more traditional geographically based approaches when considering the unit to conserve within the Ecological Paradigm.

2 | HUMPBACK WHALE EXAMPLES

Much is known about humpback whales because of the ease of identifying individuals using photographs of the unique markings on the ventral surface of their flukes, and because many of their feeding and wintering areas are within easy reach of small research vessels. Humpback whales are also easily biopsied, which has allowed thousands of genetic samples to be obtained in the North Atlantic (Palsbøll et al. 1995), the North Pacific (Baker et al. 2013), the South Pacific (Constantine et al. 2012), and elsewhere. Early studies revealed that calves learn their migratory destinations from their mothers and exhibit strong fidelity to feeding and wintering grounds throughout their lives (Clapham et al. 1993a). Humpback whales are found

on feeding grounds in summer, fall, and into early winter. Nearly all adult whales migrate to warmer waters for a few months in winter, when calving occurs. Some whales may occasionally reside year-round in some feeding areas (Straley 1990); also, there is one well-documented non-migratory population in the Arabian Sea (Pomilla et al. 2014), but this is the exception, not the rule. Studies that have accumulated around the globe for this species reveal complex migratory patterns that vary among ocean basins and are influenced by the different sizes of ocean basins and the currents within them (Kershaw et al. 2017, Rosenbaum et al. 2017). Here we focus on a few well-studied cases to argue that recruitment driven by learned migratory destinations results in all such humpback whale DIPs being migratory whale herds.

2.1 | West Indies to the Gulf of Maine migratory herd—an example of a shared wintering ground and a ‘private’ feeding ground

The western North Atlantic has several discrete humpback feeding grounds: the Gulf of Maine, the Gulf of Saint Lawrence, Newfoundland/Labrador and western Greenland (Katona & Beard 1990); additional feeding areas are located off Iceland and Norway in the central/eastern North Atlantic. The discreteness of the whales summering in these various areas is supported by photographic identification, with individually identified animals returning to the same feeding area for years or decades (Clapham et al. 1993a). It is also evident in analysis of mitochondrial DNA (mtDNA) (Palsbøll et al. 1995). Because mtDNA is inherited only from the mother, and recruitment in humpback whales is through maternal learning, this genetic marker not only provides an independent line of evidence for assessing demographic independence

and site fidelity, but also gives insight over a longer time-frame than photographic identification, and will thus be referenced in all of the examples below.

During the winter, whales from all of the western North Atlantic feeding areas (including the Gulf of Maine) mate, calve and mix spatially and socially on shared wintering grounds in the West Indies (Clapham et al. 1993b, Katona & Beard 1990, Kennedy et al. 2014, Palsbøll et al. 1997, Stevick et al. 1998). An ocean-basin scale study was conducted in 1992-1993 that provided abundance estimates of 10,600 (95% confidence interval 9,300-12,100) humpback whales in the North Atlantic (Smith et al. 1999). The estimate from the same effort for the Gulf of Maine feeding aggregation was 889 (CV = 0.32; Smith et al. 1999). Between 1999 and 2003 the average annual human-caused mortality for the Gulf of Maine was estimated to be about 4 whales (Waring et al. 2006). Should the impact of those deaths be assessed relative to the roughly 900 Gulf of Maine whales or the roughly 10,000 whales that winter in the West Indies? Given the Ecological Paradigm, which fits the objectives of the MMPA, the fact that recruitment into this feeding aggregation is via learned behavior from the females of this aggregation, the assessment of the human-caused mortality's impact should be to the 900.

However, until 2001, human-caused mortalities in the Gulf of Maine (notably fishing gear entanglements and ship strikes) were assessed against the North Atlantic abundance estimate with the calculated allowable removal at 33 whales/year (Waring et al. 2000). This allowable removal actually included a protection factor that reduced the allowable kill for endangered species by 90%. The roughly 900 Gulf of Maine whales, increasing at an estimated rate of 6.5%/year, would produce about 60 new individuals. Thus, had the allowable removal of 33 occurred, the Gulf of Maine herd could have sustained the mortalities but recovery would

have been greatly delayed. In 2002, the assessment protocol changed such that only the estimated abundance in the Gulf of Maine was used in the assessment, which reduced the allowable removal to 1.3 whales/year. The post-2001 management would have allowed, as intended, the endangered population to recover more quickly. The Gulf of Maine feeding aggregation fits the definition of a migratory whale 'herd' and is thus the appropriate 'population' to manage under the Ecological Paradigm.

Because there is substantial gene flow among the North Atlantic herds that winter in the West Indies, no significant differences in nuclear DNA were found among the western North Atlantic feeding grounds (Palsbøll et al. 1997). Using these nuclear DNA results as a basis to delineate populations of humpback whales in the North Atlantic would lead to erroneous pooling of migratory whale herds and potential mismanagement under the Ecological Paradigm. To delineate populations under the Ecological Paradigm, it is critical to evaluate the means of recruitment into the herd, which in this case does not depend on how the whales mate.

2.2 | Central America to California/Oregon/Washington herd—an example of a 'private' wintering ground and shared feeding ground

A basin-wide study of humpback whales in the North Pacific, known as SPLASH (Structure, Population Levels, And Status of Humpbacks), took place between 2004 and 2006. The study found that whales that wintered in Central America were discrete based on both photographic identification (Calambokidis et al. 2008) and mtDNA data (Baker et al. 2013) when compared with other North Pacific whales, including those that wintered in adjacent areas in

Mexico. Because the Central America animals all migrate to the same summer feeding area off the coasts of California, Oregon, and Washington, they meet the migratory whale herd definition.

Like the Gulf of Maine herd, the Central America herd was not found to differ in nuclear DNA from its nearest neighbors to the north in coastal Mexican waters, but did differ strongly in mtDNA (Baker et al. 2013). Photo-identification data from SPLASH also supported the discreteness of the Central America herd, with only 9 photographic matches between Central America (with 105 unique individuals identified) and northern coastal Mexico (with 690 unique individuals identified (Calambokidis et al. 2008). None of the 562 unique individuals identified in the Revillagigedos Archipelago were seen in Central America (Calambokidis et al. 2008). This evidence is consistent with recruitment through learning migratory destinations from mothers.

Unlike the Gulf of Maine whales, the Central America whales share their feeding grounds with whales that winter farther north along the Mexico mainland. Whales that winter in Mexico have diverse feeding ground destinations, but when the Central America whales were compared with whales that winter off Mexico and feed off California or Oregon, there were still significant differences in mtDNA (Martien et al. 2020). Within California and Oregon, the proportion of whales from these two different wintering grounds differs latitudinally, with Central America whales predominating in southern and central California, and mainland Mexico whales predominating in northern California and Oregon (Calambokidis et al. 2017a).

Documented human-caused mortality (from ship strikes and entanglements) also appear to be higher in Southern and Central California, which is an area with a large proportion of the whales that winter off Central America (Carretta et al. 2018). The abundance of the Central America

wintering aggregation during the SPLASH study was estimated as just under 800 (Wade 2021), while that of the Mexico wintering aggregation was about 2,900, though not all of the Mexico whales feed north of California and Oregon (see section 2.3). The assessment of the level of risk posed by the mortality in Central California to the Central America herd should be based upon the abundance of that herd, and the probability that a death was from that herd and not from other herds that feed in the same area (see Taylor et al. 2021 for further details in describing this herd).

2.3 | Mainland Mexico to California/Oregon/Washington herd—an example of shared wintering and feeding grounds

Based on SPLASH data, most whales from the mainland Mexico wintering aggregation migrate to feeding grounds along the contiguous U.S. west coast (California, Oregon and Washington). However, some migrate to more northerly feeding grounds in British Columbia and Alaska, with a concentration in the Aleutian Islands and Bering Sea areas. Because of ease of access by small boats, nearly continuous research along the contiguous U.S. west coast has provided good data to document the same pattern of maternally driven recruitment and site fidelity seen in the last two examples. The mainland Mexico whales that migrate to the U.S. west coast are exposed to different feeding conditions and different risks from human-caused mortality and predation compared to those who migrate to other feeding areas. They also expend different proportions of their energy budgets on migration, although it is unclear whether this is a significant factor in the energetics of the species. Martien et al. (2020) found that whales that migrate between mainland Mexico and the U.S. west coast differ in mtDNA

from the Central America herd, with which they share most of their feeding ground. In addition, Martien et al. found that this group of whales differs significantly in mtDNA haplotype frequencies from the overall mainland Mexico wintering aggregation analyzed in Baker et al. (2013), which contains whales with multiple feeding destinations. Thus, the whales that migrate between mainland Mexico and the U.S. west coast fit the migratory whale herd definition, with maternally-driven recruitment and strong fidelity to both feeding and wintering grounds.

This herd shares their wintering grounds with whales that feed on more northerly feeding grounds, and shares their feeding grounds with Central America whales. Human-caused mortalities off Central California should not be assessed against those whales that winter along the Mexico mainland but which migrate to more northerly waters (see Martien et al. 2021 for further details in describing this herd). Appropriate assessment of the death of a whale of unknown population origin killed off California would use data from two migratory whale herds: Central America, and the herd from mainland Mexico that feeds along the contiguous U.S. west coast.

2.4 | Hawai'i to Southeast Alaska migratory whale herd—an example of a shared wintering ground and nearly private feeding ground

Whales that winter in the Hawai'ian Archipelago migrate, in various proportions, to feeding grounds that span the North Pacific Basin. Nearly all these feeding grounds are to a greater or lesser extent shared with whales from other wintering grounds. The exception is the Southeast Alaska feeding ground, which during the SPLASH years (2004-2006) was occupied almost entirely by animals from Hawai'i (Wade 2017 estimated that only 2% originated from

Mexico). The Hawai'i-Southeast Alaska migratory herd is of interest for two reasons: 1) the overall nuclear DNA profile of Southeast Alaska differs from that found in the Hawai'i wintering ground, where the herd is mixed with herds from multiple feeding grounds (Baker et al. 2013), and 2) only five mtDNA haplotypes have been found in Southeast Alaska whales, with over 96% of individuals possessing the two most common haplotypes. In comparison, Baker et al. (2013) detected 11 haplotypes in Hawai'i, with the two most common comprising only 71% of the population. The first point is of interest because it suggests that some mating may occur on the migratory route. If nearly all Southeast Alaska whales migrate to Hawai'i and all mating occurred in Hawai'i when whales from many feeding areas are present, then nuclear DNA differences would not be expected. Until there is a better understanding of when and where mating occurs, the wintering area cannot be assumed to be the only place where breeding occurs.

From the perspective of the migratory whale herd concept, the second finding – that 96% of the Southeast Alaska herd has only two haplotypes – is of great interest because it yields insight into the long-term stability of the herds. Shore-based whaling killed humpback whales in Southeast Alaska in the early 1900s (Andrews 1909) but ceased by 1922 (Rice & Wolman 1975). By 1986 Baker et al. (1992) estimated 547 whales (95% CL 504-590) in Southeast Alaska. By 2005 the estimate exceeded 2,000 whales (Wade 2017). Haplotypic diversity (h) is the probability that two individuals randomly sampled from the same population will have different haplotypes. Haplotypic diversity is relatively high for all feeding areas combined ($h=0.81$) but is very low ($h=0.47$) for Southeast Alaska (Baker et al. 2013). The five haplotypes found in Southeast Alaska compares with 11 in Hawai'i and 14 in the northern Gulf

of Alaska. The most common haplotypes in Southeast Alaska (A- and A+; Baker et al. 2013) are uncommon in California and Oregon, and the most common haplotype in California and Oregon (F2; Baker et al. 2013) is completely absent from Southeast Alaska. The most parsimonious explanation for most whales in Southeast Alaska sharing one of two common haplotypes is that recovery from the low numbers following whaling was completely through recruitment of mothers teaching their calves the migratory route from Hawai'i to Southeast Alaska likely in conjunction with whaling-induced stochastic lineage extinction. Thus, this strong maternal fidelity and natal philopatry has lasted at least over several whale generations.

2.5 | General conclusions from humpback whale examples

The four examples of humpback migratory herds presented above illustrate every combination of shared and private feeding grounds and wintering grounds, with the exception of one-to-one private wintering and feeding grounds. Having both mixed feeding grounds and wintering grounds makes any stratification based on geography problematic, and has contributed to debate regarding humpback population structure, particularly in the North Pacific (Baker et al. 1994, Baker et al. 2013, Barlow et al. 1997, Calambokidis et al. 2008, Calambokidis et al. 2001, Darling et al. 2022, Darling & McSweeney 1985, Donovan 1991). While it has been suggested that the low-level of interchange between the Mexico and Hawai'i wintering grounds might support a hypothesis of panmixia throughout the North Pacific (Darling et al. 2022), the low level of exchange found to date (e.g., from SPLASH 17/2317 = 0.7% of whales identified in Hawai'i were also seen in Mexico; Calambokidis et al. 2008) is likely to have no demographic impact and minimal genetic influence if animals fail to breed during these relatively rare excursions.

Though the wintering grounds remain the presumptive breeding unit for humpback whales, the fact that animals spend the majority of the year on their feeding grounds suggests feeding aggregations as the more appropriate choice for studies focused on ecological processes. Much of the debate concerning population structure in humpback whales hinges on this feeding vs. wintering ground dichotomy, while the herd concept recognizes that it is the combined fidelity to both feeding and wintering grounds that shapes population structure in humpback whales.

Assessing the impact of human-caused mortality should be based upon the migratory whale herd since it is the demographically independent population (DIP). The migratory whale herd concept should also change the way ecological and demographic analyses are conducted. For example, Martien et al. (2020) chose to use genetic samples from biopsied individuals that had been photographically identified on both the feeding and wintering grounds. Those samples can be assigned to a migratory herd and can therefore be used to calculate allele frequencies of 'pure stocks' in a mixed stock analysis (Utter & Ryman 1993). Within the North Pacific, the only known geographic stratum that represents a 'pure stock' is the Central America wintering aggregation, which is comprised of a single herd. However, even in that case stratifying by geography is problematic because data collected since the SPLASH study suggest that the Central America wintering aggregation extends into southern Mexico, and may overlap in range with the herds that winter along the coast of northern Mexico (Martinez-Loustalot et al. 2020, Ortega-Ortiz & Authors In press).

Nonetheless, there is reason to be optimistic that humpback herds can be delineated in the near future. The advent of highly accurate automated matching algorithms that use

photographs from researchers and citizen scientists has dramatically increased the number of individuals for which both the wintering and feeding ground, and therefore the herd affiliation, are known (Cheeseman et al. 2021). The large number of biopsy samples available from photographed animals makes it likely that once the match of photographic data sets is complete, herd affiliations can be determined, enabling the assessment of genetic differentiation between and genetic assignment to herds. Geographic areas with higher human impacts are likely to be the areas with the most detailed data available.

3 | GRAY WHALE EXAMPLES

Another species with population structure consistent with the migratory whale herd concept is the gray whale. Gray whales use three primary feeding areas within the North Pacific: 1) the northern feeding ground (NFG), which includes waters of the northern Bering, Chukchi, and Beaufort Seas and is used by the majority of whales (~20,000; Stewart & Weller 2021); 2) the Pacific Coast Feeding Group (PCFG) feeding ground, which includes waters from northern California through southeastern Alaska and is regularly used by a small number of whales (~230, Calambokidis et al. 2019) (Darling 1984, Calambokidis, 2002 #1377, Gilmore 1960, Hatler & Darling 1974, Pike 1962); and 3) the Sakhalin Island (SI) feeding ground, which is located off the northeastern coast of Sakhalin Island, Russia, in the Okhotsk Sea/western North Pacific (WNP; Burdin et al. 2021, Meier et al. 2007, Weller et al. 2002, Weller et al. 1999) and is used by a small number of whales (102-144 mature whales, Cooke et al. 2018). Smaller concentrations of feeding whales can be found off the southern and southeastern coast of Kamchatka, Russia, which is used by at least some of the same whales that feed off Sakhalin

(Burdin et al. 2011, Tyurneva et al. 2010, Vertyankin et al. 2004). The majority of whales, including all of those from the NFG and PCFG feeding grounds, overwinter in the lagoons and coastal waters off Baja Mexico, while a much smaller number of whales are thought to overwinter in the WNP wintering ground (discussed below). Here we restrict our evidence for the migratory herd concept in gray whales to those areas where photographic identification and genetic data are available to assess population structure patterns.

3.1 Western North Pacific wintering ground to Sakhalin Island—an example of a private wintering and a shared feeding ground

The strongest evidence of matrilineal fidelity to feeding areas comes from long-term photo-identification studies of the whales using the SI feeding ground in the western North Pacific (WNP; Bradford et al. 2006, Weller et al. 2002, Weller et al. 1999). After the initial years of study, the majority of ‘new’ (i.e., previously unidentified) whales photographed on the SI feeding ground have been calves brought to the area by known SI mothers. As the study has continued, it has been possible to document the next generation of fidelity, as several of those female calves have now matured and returned to the area with their own calves (e.g., Burdin et al. 2021). In addition, a model-based assessment incorporating the photo-identification data found that the group of whales feeding off SI is, at least in recent years, self-contained, such that most or all of the animals recruited into the population are the calves of SI mothers (Cooke et al. 2013, Cooke et al. 2017).

The mtDNA data provides further evidence that this pattern has persisted over multiple generations (Lang et al. 2021, LeDuc et al. 2002). Although a relatively large number of mtDNA

control region haplotypes (n=22) are found among whales sampled off Sakhalin, a high proportion (69%) of the SI whales, including most known reproductive females, carry one of two haplotypes. Three additional haplotypes are found at moderate frequencies, including two which are carried by known mothers, and whose frequencies have grown over time. The remaining haplotypes are found only in a single individual, all of which are males.

Correspondingly, the haplotype diversity found among the Sakhalin whales ($h=0.760$) is markedly lower than that found among whales sampled on the feeding and wintering areas in the ENP ($h=0.952$). The same is true when full mitogenomes are examined (Sakhalin $h=0.723$, ENP $h=0.975$; Brüniche-Olsen et al. 2021, Meschersky et al. 2015).

The exact location of the wintering ground(s) in the WNP remains unknown. Records from sightings, strandings, and historical whaling catches indicate that at least some gray whales occurred in the coastal waters off China in the South China Sea (see review in Weller et al. 2002), although only two records of gray whales in these waters have been reported in the last 25 years (Wang et al. 2015, Zhao 1997, Zhu 2012). While all of the whales feeding off SI were originally presumed to overwinter in the WNP (i.e. South China Sea region), recent evidence indicates that nearly half (~48%; Cooke 2020) of these whales migrate to the ENP, where they overwinter in the lagoons and coastal waters off Baja Mexico (Mate et al. 2015, Urbán 2019, Weller et al. 2012). This separate migratory herd (WNP to ENP) is considered below. The remaining 52% of the whales feeding off Sakhalin are not thought to use the Mexico wintering ground (Cooke 2020) and are presumed to remain in the WNP year-round. This is substantiated by records of sightings, strandings, and entanglements of gray whales in Japanese waters (Nakamura et al. 2021); most of these records, which include those from at least two

whales that were first identified as calves with their mothers on the SI feeding ground (Weller et al. 2008, Weller et al. 2016), are from months when whales would likely be migrating. In addition, the U.S. Navy has recorded what are possibly gray whale calls in the East China Sea region; the timing and direction of these calls were consistent with small numbers of whales migrating south and north through the area (Gagnon 2016). One of the two whales matched between Sakhalin and Japan was photographed in Japanese waters during winter and spring of multiple years (Weller et al. 2016), providing some evidence of fidelity to WNP migratory paths and wintering destination(s).

Unlike the whales that migrate between Mexico and Sakhalin, little is known about the identity of the SI whales that remain in the WNP year-round. Consequently, although a high proportion of the whales that feed off SI have been biopsied (Lang et al. 2021), it is not possible to make genetic comparisons of SI whales that overwinter in the WNP with other groups.

3.2 Mexico lagoons to Sakhalin — a case of shared wintering and feeding areas

The case for site-fidelity to Sakhalin has been made above. Photo-identification and satellite tracking data have shown that 54 gray whales known to show fidelity to the WNP SI feeding ground have also been recorded using the ENP wintering ground off Baja Mexico (Mate et al. 2015, Urbán 2019, Weller et al. 2012). Some of these whales have been photographed in the Mexico lagoons in multiple years (Urbán 2019), providing some evidence of fidelity to this wintering ground. Six SI whales have been photographed off southern Vancouver Island, British Columbia, during the northbound migration from Mexico to Sakhalin; all of these sightings occurred on only two days, with three whales sighted as part of a single group on one day and

the other three whales sighted in two groups in close proximity to each other on a single day (Weller et al. 2012).

Significant nuclear genetic differences have been found when comparing the SI whales with the whales that feed on the NFG (Lang et al. 2021) as well as with whales sampled on the Mexico wintering grounds (Brüniche-Olsen et al. 2018), indicating a lack of random mating between these groups. These genetic differences remain apparent when only those SI whales known to overwinter in Mexico are compared to the NFG whales (Lang et al. 2021). The data available on gray whale reproduction, which is largely based on whales taken under scientific permit whaling off the coast of central California in the late 1950s and 1960s, suggest that most mating takes place during migration, with conception thought to primarily occur during a three-week period from late November to early December (Rice & Wolman 1971). For the whales migrating between Sakhalin and Mexico, this mating period may occur before the SI whales join the southbound migration of NFG whales, potentially providing a mechanism for SI whales to largely (but likely not exclusively, see Brüniche-Olsen et al. 2018, Lang et al. 2021) interbreed with each other and creating the signal of nuclear genetic differentiation that has been observed.

3.3 Mexico lagoons to the Pacific Northwest Coast —a case of a shared wintering and semi-private feeding areas

Patterns of fidelity to the PCFG feeding area in the eastern North Pacific (ENP) are more complex. This area is used by two categories of whales, one that is comprised of whales that return frequently to this feeding ground and account for the majority of sightings, and another

that consists of individuals seen only in one year and generally for shorter time periods and in more limited areas (Calambokidis et al. 2002, Calambokidis et al. 2019). Individuals in the first category are considered to be part of the Pacific Coast Feeding Group, while those in the second category appear to be individuals that have deviated, temporarily, from the northward migratory route and that otherwise feed on the NFG. The IWC considers whales that are seen in two or more years during the feeding season (June through November) within the region extending from northern California through northern British Columbia to be part of the PCFG (Commission 2011). These whales show a wide range of annual sighting patterns, with some being sighted in most years while others are sighted more sporadically. Photo-identification studies of the PCFG whales indicate matrilineal fidelity to the PCFG feeding ground: 65% of the whales first identified as calves with known PCFG mothers have been sighted on the feeding ground in subsequent years (Calambokidis et al. 2017b). This level of feeding area philopatry for PCFG calves is close to the estimated value of 70% for first-year survival (Bradford et al. 2006). However, new non-calf individuals are sighted each feeding season, many of which return to the area to feed in subsequent years and are thus considered to have been recruited into the PCFG. While some of these whales may be individuals born to PCFG mothers but not identified as calves prior to weaning, they may also be whales that fed in other areas in previous years. One whale sighted within the PCFG feeding area over three years was subsequently photographed off Barrow, Alaska, demonstrating that at least some whales seen in repeat years in the PCFG area at least occasionally use other feeding areas (Calambokidis et al. 2012).

The more complex pattern of matrilineal fidelity to the PCFG feeding ground can also be seen in the mtDNA genetic data. Comparisons of PCFG whales with NFG as well as with whales

sampled on the migratory route have revealed significant mtDNA differences, consistent with the occurrence of matrilineal fidelity (Frasier et al. 2011, Lang et al. 2014). However, the magnitude of those differences is relatively low when compared to that seen between SI whales and NFG whales, and the haplotype diversity found among PCFG whales is slightly lower than, but similar to, that found in the NFG.

There have been 15 cases where PCFG whales were photographed in a group of multiple whales while migrating off southern California. Nine of these groups included more than one PCFG whale, with five cases where between three and five PCFG whales were part of the same group (Calambokidis & Perez 2017). In five of the nine cases, one or more non-PCFG whales were also part of the group. Six of these nine groups were migrating south, including a group that was photographed with at least five PCFG whales off Southern California (i.e., Palos Verdes Peninsula) in mid-December 2013.

3.4 General conclusions from gray whale examples

Like the humpback whale examples, stratification of gray whale data based on geography alone is problematic. The two herds that feed in the WNP face shared risks during the summer feeding season, including entrapment in salmon fishing trap nets (Lowry et al. 2018) and potential disturbance or injury due to oil and gas activities, including associated vessel traffic, off SI (Silber et al. 2021, Weller et al. 2002). Further, they face unique risks while migrating, and presumably also while on their different wintering grounds; the whales migrating from SI to the WNP wintering ground must navigate past high-volume commercial seaports along the coast of Asia and through areas with extensive use of gill nets and set-nets in

the coastal waters of Japan (Lowry et al. 2018, Silber et al. 2021). The whales migrating from SI to wintering areas in the ENP (e.g. Mexico) also travel through regions with apparently high risk of vessel interactions, and traverse two areas known to have high killer whale predation on gray whale calves (Barrett-Lennard et al. 2011, Goley & Straley 1994, Silber et al. 2021). Whales that feed off SI and winter in Mexico undertake one of the longest migrations of any mammal (on the order of 22,000 km round trip; Mate et al. 2015), and are estimated to have higher mean energy requirements than whales migrating between Mexico and the NFG (Villegas-Amtmann et al. 2017). PCFG whales, which have a markedly shorter migration between the Pacific Northwest and Mexico, also face unique risks, including spending the summer and early fall feeding in an area where large commercial fishing and shipping ports are located and shipping traffic is pronounced (Lagerquist et al. 2019, Silber et al. 2021). Although we did not discuss the most abundant group of gray whales that summers in the Chukchi and Bering Seas, they are likely to experience the greatest changes to their habitat from global warming.

4 | CONCLUSIONS

The coastal habits of humpback and gray whales has made possible the accumulation of photographic and genetic data that facilitated the development of the migratory whale herd concept. However, this model of population structure likely applies to other whale species as well. Many large migratory whales share the life history trait of substantial maternal investment necessitating a nursing period that spans the mothers' return migration to their feeding grounds. The resulting maternally inherited migratory route, together with strong fidelity to wintering and summering areas, are defining characteristics of the migratory whale herd. We

suggest that if migratory whales have female-directed learning of the migratory route, the default assumption should be that the migratory whale herd is the demographically independent unit. We have demonstrated that management under the ecological paradigm is improved through treating these herds as the unit to conserve.

For species that are not as easily studied as humpback and gray whales, delineating herds will involve not only assuming that the herd hypothesis is the correct starting point but also thinking creatively about what data can be brought to bear. For some species with more offshore distributions and often unknown wintering areas, obtaining sufficient photographic identification or genetic data may be infeasible. Prioritizing delineation of herds with the greatest conservation and management needs may be necessary in these cases. Delineating those herds may require bringing together scientists with a range of expertise, and will facilitate integration of the best available scientific data for the purpose of DIP delineation, as required under the MMPA (Martien et al. 2019).

For example, fin whales (*Balaenoptera physalus*) are difficult to photograph and biopsy and often inhabit areas with few known anthropogenic threats (Edwards et al. 2015, Mizroch et al. 2009). However, those that spend time off the U.S. west coast face high ship-strike threat in some or all of the year (Rockwood et al. 2017). Data that are currently available, or will be available in the next few years, have been deemed sufficient for re-evaluating population structure within this area (Appendix 4 in Martien et al. 2019). Acoustic data suggest calls found from several different feeding grounds are present across the North Pacific during the winter (Archer et al. 2019, Oleson et al. 2014, Širović et al. 2013). If research is aimed at delineating migratory whale herds, any sampling in winter would require that genetic data be coupled with

acoustic data or some other data indicative of feeding grounds (perhaps stable isotope or pollutant data) for the purpose of stratifying by potential herds. Even before reliable delineation is possible, if the migratory whale herd is adopted as the Unit to Conserve, then ship strikes in winter can potentially be allocated according to the proportion of calls from each feeding group, assuming call rates are comparable (see Monnahan et al. 2014 for an example with blue whales). Monitoring of ship strikes and other human-caused mortality based on feeding group call representation would allow for immediate assessment of possible herd-specific threats.

A parting thought involves consideration of shifts in migratory whale herd ranges as large whales recover from whaling, and as habitats are altered as a result of climate change. Population structure that is mediated by learned behavior can be expected to change more rapidly than population structure defined by geographical constraints. While most biologists will expect shifting population structure as challenges to a long-lived species change, it may be more difficult to communicate these responsive shifts to managers and others that rely on the same resources as large whales for their livelihoods. Conservation will benefit from good communication with stakeholders who will be affected by adopting the migratory whale herd concept and, in turn, moving away from the more static geographically defined population concept.

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